

Dendrobium (Orchidaceae): To split or not to split?

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ABSTRACT. *Dendrobium* Sw. is one of the three largest orchid genera, with around 1580 species if certain currently accepted satellite genera are included. Until recently, no serious attempts have been made to split up this important genus into smaller genera. An infrageneric classification at the sectional level, largely due to Schlechter, has been accepted by most workers. Recent analyses based on DNA markers by Yukawa, Clements, and others have provided new insights into the phylogeny of *Dendrobium*. Their work shows that *Dendrobium* is not monophyletic when the satellite genera are excluded. This led to proposals to split up *Dendrobium* into as many as fifty genera, largely along the lines of Schlechter's sections. However, the data do not suggest any single, evident way to do the splitting. Here it is argued that a broad concept of the genus *Dendrobium*, which includes genera like *Cadetia* Gaudich., *Flickingeria* A.D.Hawkes and *Epigeneium* Gagnep., among others, is to be preferred. The comparable cases of other large orchid genera are briefly discussed and some observations are made on character evolution in *Dendrobium* and the origin of the genus in light of DNA-based phylogenies.

Keywords. Classification, *Dendrobium*, generic concepts, molecular phylogeny, Orchidaceae

Introduction

In its traditional, broad delimitation, *Dendrobium* Sw. is one of the three largest orchid genera (Cribb & Govaerts 2005: 1197 spp.) as well as one of the most important in commercial horticulture. Certain species of this genus are in high demand in traditional Chinese medicine, which puts wild populations of these species under pressure from (illegal) collecting in China and neighbouring countries. Habitat destruction threatens the survival of many more species throughout the range of the genus. The taxonomy of *Dendrobium* is therefore of interest not only to botanists, but also to orchid growers, ecologists and conservationists.

Dendrobium belongs to subtribe Dendrobiinae in the tribe Dendrobieae of the subfamily Epidendroideae, the largest of the five subfamilies within the Orchidaceae. Most species of *Dendrobium* are epiphytes in primary forest, less often lithophytes; only very few are obligate terrestrials. The range of the genus extends from Sri Lanka and India throughout tropical Asia, north to Japan, east to Tahiti, and south to New Zealand.

Prior to the advent of molecular methods, various classifications had been proposed for *Dendrobium* and related genera, as summarised in Wood (2006). Dressler

(1981, 1993) expressed a consensus view when he listed six genera as constituting the subtribe Dendrobiinae: *Cadetia* Gaudich., *Dendrobium*, *Diplocaulobium* (Rchb.f.) Kraenzl., *Epigeneium* Gagnep., *Flickingeria* A.D.Hawkes (*Ephemerantha* P.F.Hunt & Summerh.), and *Pseuderia* Schltr. In this view, the Dendrobiinae consist of the very large and complex genus *Dendrobium* next to a number of much smaller, more homogenous genera, which had all been treated as sections of *Dendrobium* in the past. Rudolf Schlechter (1911–1914) must be credited with presenting an infrageneric classification of *Dendrobium* that has been adopted with few modifications by most subsequent workers. This, however, applies only to the section level. Schlechter's system of subgenera is almost entirely artificial, being based on the application of single defining character states, such as the presence or absence of a sheathing leaf base. As we now know, this does not lead to phylogenetically meaningful groupings in this subtribe.

The pioneering studies by Yukawa and co-workers (1993, 1996, 2000, 2001) using DNA markers (matK and ITS) have provided a number of insights, which were confirmed and extended by later studies (Clements 2003, 2006; Wongsawad et al. 2005; Burke et al. 2008; Sathapattayanon 2008):

1. Dendrobiinae consists of three main clades:

- I. A predominantly continental Asian and West Malesian clade that includes the type species of *Dendrobium* (*D. moniliforme* (L.) Sw.).
- II. A predominantly East Malesian - Australian - New Caledonian clade that includes, e.g., *D. bigibbum* Lindl., as well as *Cadetia*, *Diplocaulobium* and *Flickingeria*.
- III. A much smaller clade that consists of the genus *Epigeneium*.

Following Clements (2003), these clades will here be referred to as the Asian, Australasian and *Epigeneium* clade respectively.

2. Under the consensus classification, *Dendrobium* is polyphyletic.

Yukawa et al. (1993) found that the genus *Pseuderia* is not a member of the Dendrobiinae, but appears to belong to the tribe Podochileae. In view of the deviating vegetative and floral morphology of *Pseuderia*, both within Dendrobiinae and Podochileae, its placement within the subfamily Epidendroideae needs further study. In addition, Clements (2003) showed that a group of species traditionally treated as section *Oxystophyllum* of *Dendrobium* properly belongs in the subtribe Eriinae.

The taxonomic implications of these molecular studies found their expression in two highly divergent views. Some authors presented arguments in favour of a very large, monolithic and monophyletic genus *Dendrobium*, essentially comprising the whole subtribe Dendrobiinae, except perhaps the genus *Epigeneium* (Yukawa 2001, Burke et al. 2008). On the other hand, Clements & Jones (2002), in line with an earlier suggestion by Yukawa et al. (1993), proposed that *Dendrobium* should be split up in several smaller genera. Clements (2006) recognises as many as 50 genera in this alliance. According to Clements (2003), the three main clades should be treated as distinct subtribes (I: Dendrobiinae, II: Grastidiinae, and III: Epigeneiinae). Wood (2006), while provisionally following Dressler's consensus view (except for *Pseuderia*

and *Oxystophyllum*), expressed the hope that a middle ground between extreme lumping and extreme splitting could be found.

Material and methods

The phylogram here shown (Fig. 1, 2) is based on sequences of the Internal Transcribed Spacer 1 (partial), 5.8S ribosomal RNA gene (complete), and Internal Transcribed Spacer 2 (partial) downloaded from GenBank (<http://www.ncbi.nlm.nih.gov>). See Table 1 for taxa and accession numbers. Taxa were selected to make the analysis comparable to earlier studies by Clements (2003, 2006) and Yukawa (2001). Where possible, different but morphologically similar species were chosen. When a taxon was represented by multiple accessions, initially all accessions were included

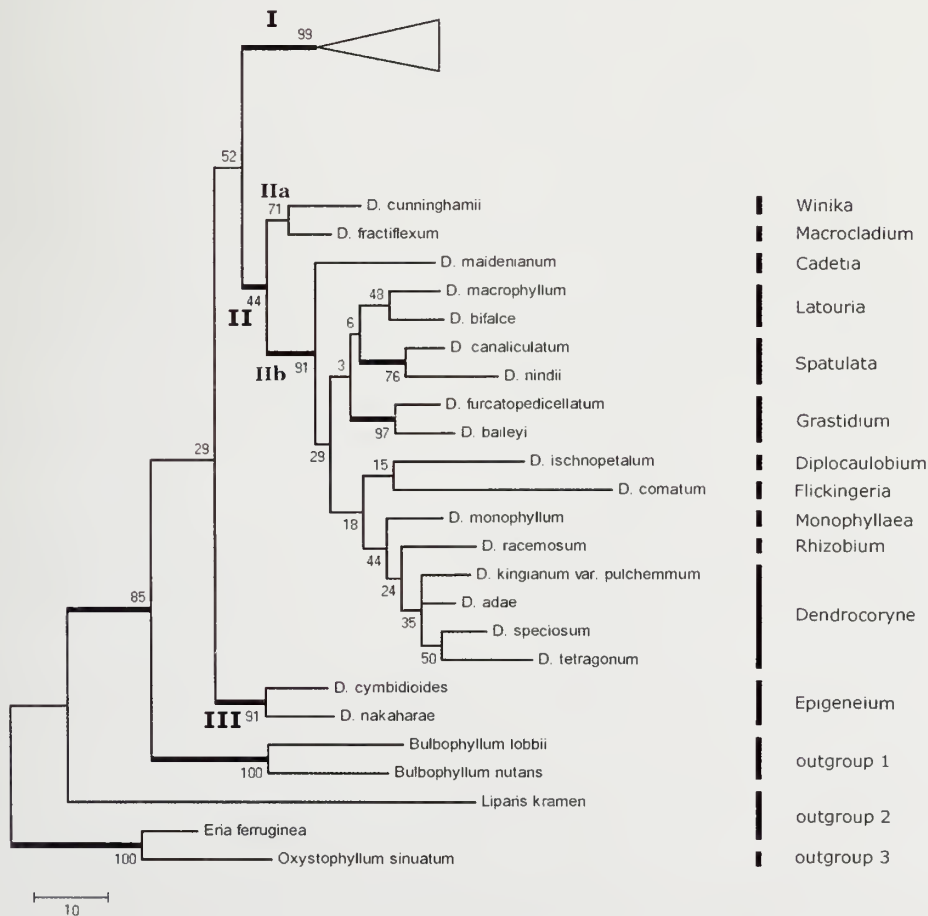


Fig. 1. One of 20 most parsimonious phylograms of selected *Dendrobium* species based on ITS sequence data. Names on the right refer to the traditional sections and genera in which the species would be included. Clade I is shown in Fig. 2.

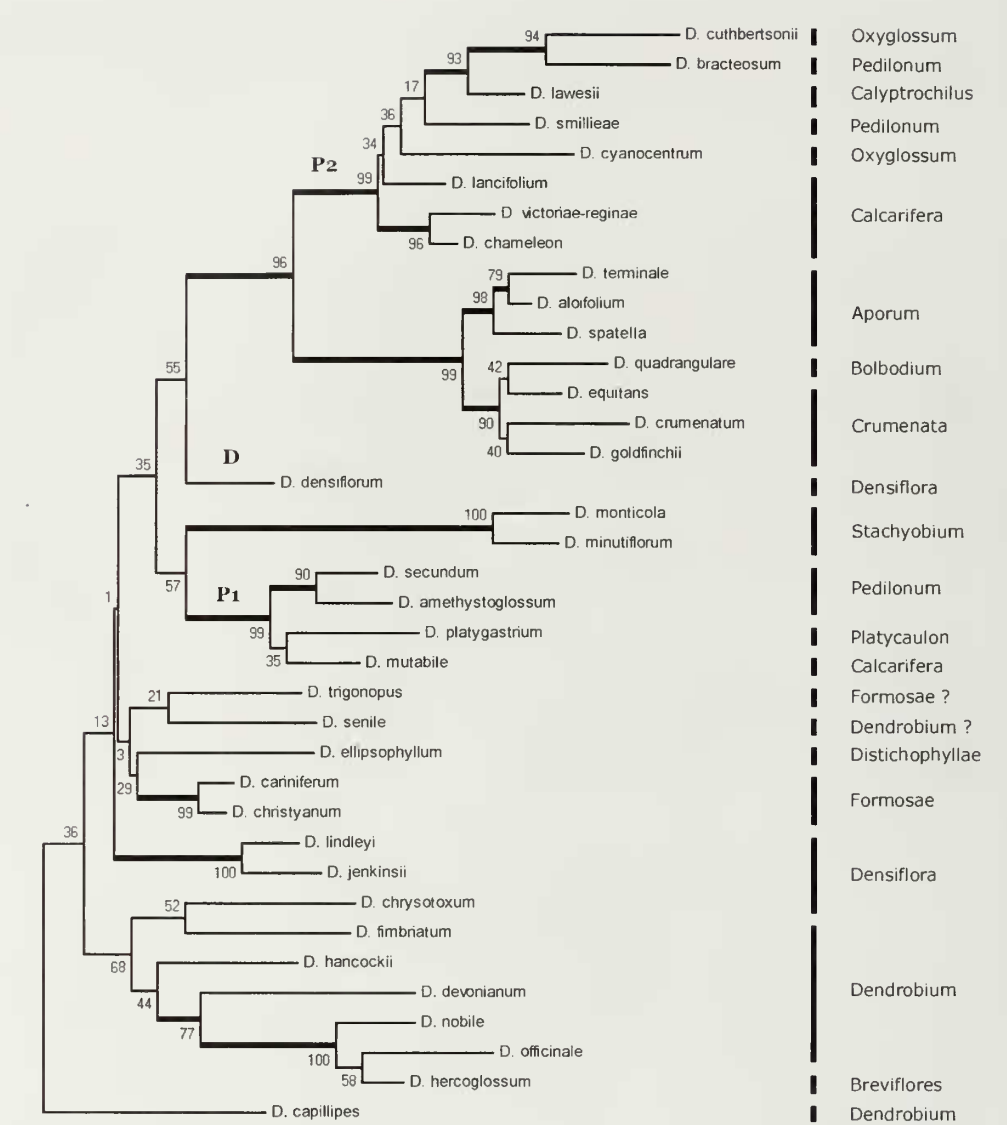


Fig. 2. Phylogram of Clade I (from Fig. 1).

in the alignment. In all cases these accessions gave identical results during phylogeny inference, although there often were minor differences between the sequences, for example in the three accessions of *D. chrysotoxum* Lindl. Afterwards one accession was chosen arbitrarily to represent the taxon. Unfortunately, Yukawa's and part of Clements's sequence data were not yet uploaded to GenBank at the time of this study.

A number of motif-based tests for the detection of pseudogenes were performed (Harpke & Peterson 2008, Feliner & Rosselló 2007). Sequences were aligned with Mega version 4 (Tamura et al. 2007), using the ClustalW algorithm, and adjusted manually. The phylogeny of the 61 selected taxa was inferred with Mega4, using maximum parsimony with the following options: close-neighbour interchange,

Table 1. List of GenBank accession numbers.

<i>Bulbophyllum lobbii</i> Lindl. – EF195931; <i>B. nutans</i> Thouars – EF196038; <i>Dendrobium adae</i> F.M.Bailey – EU430371; <i>D. aloifolium</i> (Blume) Rchb.f. – AY239951; <i>D. amethystoglossum</i> Rchb.f. – AY239952; <i>D. baileyi</i> F.Muell. – AY240016; <i>D. bifalce</i> Lindl. – EU430373; <i>D. bracteosum</i> Rchb.f. – AY239954; <i>D. canaliculatum</i> R.Br. – EU430375; <i>D. capillipes</i> Rchb.f. – AF362035; <i>D. cariniferum</i> Rchb.f. – AF362027; <i>D. chameleon</i> Ames – AF521607; <i>D. christyanum</i> Rchb.f. – EF629325; <i>D. chrysotoxum</i> Lindl. – EU477501; <i>D. comatum</i> (Blume) Lindl. – AB289469; <i>D. crumenatum</i> Sw. – AF521608; <i>D. cunninghamii</i> Lindl. – AY240019; <i>D. cuthbertsonii</i> F.Muell. – AY239950; <i>D. cyanocentrum</i> Schltr. – AY239964; <i>D. cyubidioides</i> (Blume) Lindl. – AY240011; <i>D. densiflorum</i> Wall. ex Lindl. – DQ058786; <i>D. devonianum</i> Paxton – FJ384735; <i>D. ellipsophyllum</i> Tang & F.T.Wang – AF362033; <i>D. equitans</i> Kraenzl. – AF521609; <i>D. fimbriatum</i> Hook. – EU003116; <i>D. fractiflexum</i> Finet – AY239949; <i>D. furcatopedicellatum</i> Hayata – AF521611; <i>D. goldfinchii</i> F.Muell. – AY239969; <i>D. hancockii</i> Rolfe – EU003120; <i>D. hercoglossum</i> Rchb.f. – AF363685; <i>D. ischnopetalum</i> Schltr. – AY240007; <i>D. jenkinsii</i> Wall. ex Lindl. – DQ058785; <i>D. kingianum</i> var. <i>pulcherimum</i> Rupp – EU430385; <i>D. lancifolium</i> A.Rich. – AY239976; <i>D. lawesii</i> F.Muell. – AY239977; <i>D. lindleyi</i> Steud. – DQ058784; <i>D. macrophyllum</i> A.Rich. – AY239979; <i>D. maidenianum</i> Schltr. – AY239948; <i>D. minutiflorum</i> S.C.Chen & Z.H.Tsi (= <i>D. sinominutiflorum</i> S.C.Chen, J.J.Wood & H.P.Wood) – DQ058800; <i>D. monophyllum</i> F.Muell. – EU430387; <i>D. mouticola</i> P.F.Hunt & Summerh. – DQ058798; <i>D. mutabile</i> (Blume) Lindl. – AY239984; <i>D. nakaharae</i> Schltr. – AF521618; <i>D. nindii</i> W.Hill – AY239985; <i>D. nobile</i> Lindl. – EU477507; <i>D. officinale</i> Kimura & Migo (= <i>D. catenatum</i> Lindl.) – EU592018; <i>D. playgastrum</i> Rchb.f. – AY239955; <i>D. quadrangulare</i> Parish & Rchb.f. (= <i>D. hymenanthum</i> Rchb.f.) – EU840698; <i>D. racemosum</i> (Nicholls) Clemesha & Dockrill – EU430389; <i>D. secundum</i> (Blume) Lindl. – AY239993; <i>D. senile</i> Parish ex Rchb.f. – EU477509; <i>D. smillieae</i> F.Muell. – AY239996; <i>D. spatella</i> Rchb.f. – AF362034; <i>D. speciosum</i> Sm. – EU430399; <i>D. terminale</i> Parish & Rchb.f. – DQ058801; <i>D. tetragoum</i> A.Cunn. – EU430403; <i>D. trigonopus</i> Rchb.f. – DQ058793; <i>D. victoriaereginae</i> Loher – EU840694; <i>Eria ferruginea</i> Lindl. – AF521071; <i>Liparis krameri</i> Franch. & Sav. – AB289469; <i>Oxystophyllum sinuatum</i> (Lindl.) M.A.Clem. – AY239995.
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search level 3, with 50 random addition tree replications. Tree support was tested using bootstrapping with 1000 replications. Gaps were treated as missing data ('include all sites' option in Mega4). For various small subsamples of the taxa parsimony analyses were conducted using the exhaustive max-mini branch-and-bound algorithm in Mega4. These analyses produced tree topologies that were consistent with the ones found in the complete analysis.

Results

A. Testing for pseudogenes

Harpke & Peterson's test motif CGATGAAGAACGyAGC is not found in any species included in this study; all have CGATGAAGACCGCAGC instead (absence of the test motif indicates potential pseudogene). On the other hand, the test motif GAATTGCAGAAwyC is present in all species except in *D. hancockii*, which has

AAATTGCAGAATCC. The motif GGCry-(4 to 7n)-GyGyCAAGGAA (Feliner & Rosselló 2007) was found only in *Eria ferruginea* Lindl., *D. mutabile* Blume and *D. maidenianum* Schltr. The motif GAATTGCAGAATTC, unlike the more general GAATTGCAGAAwC recommended by Harpke & Peterson, was not found in any species, all had GAATTGCAGAATCC, except for *D. hancockii* Rolfe, which had AAATTGCAGAATCC. A conserved EcoRV site, GATAC, was not present in *D. nobile* Lindl., *D. officinale* Kimura & Migo (= *D. catenatum* Lindl.), *D. hercoglossum* Rchb.f., *D. victoriae-reginae* Loher and *D. chameleon* Ames; these all had GATAT. These results show that further testing for pseudogenes is indicated for all the species included in this study, and that at least the sequence for *D. hancockii* here used is likely to be a pseudogene. According to Burke et al. (2008) the inclusion of pseudogenes did not have a significant influence on the phylogeny inferred in their study, except that longer branch lengths were found as a result. They identified the sequence of their accession of *D. baileyi* F.Muell., also used in the present study, as a potential pseudogene. In theory, the use of paralogous sequences could influence the inferred phylogeny considerably. However, in *Dendrobium* strongly supported results using matK are usually replicated with strong support when using ITS (Wongsawad et al. 2005, Sattapattayanon 2008), and vice versa. This suggests that these results are not much distorted by the inclusion of pseudogenes, or paralogous sequences in general. The position of *D. hancockii* in Fig. 2 is in agreement with its membership of section *Dendrobium* on morphological grounds. Likewise, *D. baileyi* nests with another member of section *Grastidium*, as expected (Fig. 1). Nevertheless, the fact that quite a few species of *Dendrobium* are unplaced, as discussed below, may indicate that the role of pseudogenes and other genetic factors, such as ancient hybridization, need further study.

B. Phylogeny

The aligned sequences had a length of 747 sites (including gaps), of which 395 were parsimony informative. One of the 20 most parsimonious trees (length 2409, consistency index 0.404, retention index 0.619) is shown here (Fig. 1, 2). In its general topology it agrees well with earlier studies by Yukawa and co-workers (Yukawa 2001, Yukawa & Uehara 1996, Yukawa et al. 1993, 1996, 2000), Clements (2003, 2006) and Burke et al. (2008). In line with these studies, three main clades (marked I, II and III) can be distinguished in the ingroup. It is seen that *Cadetia*, *Flickingeria* and *Diplocaulobium* are all nested within the Australasian clade (II), demonstrating that recognition of these genera while maintaining *Dendrobium* in the broad sense renders the latter paraphyletic, as first noted by Yukawa et al. (1993). The Asian clade (I) generally shows longer branches than the Australasian clade. In the Asian clade the average number of changes from the nearest node common to clade I and II to a terminal node is 65.2; in the Australasian clade this is 28.9 changes.

The following discussion includes the results of the studies cited above. Some of the sections and species mentioned below are not found in the phylogram shown here because there were no sequences available from GenBank for these.

In contrast to most other studies, bootstrap support for the *Dendrobium* clade as a whole was here found to be low. No clear grounds for this anomaly could be detected. The *Epigeneium* clade (III) is well supported; it is basal to the two other clades, of which the Asian clade (I) has very strong bootstrap support here as well as in all studies cited. The Australasian clade (II) is less strongly supported, as is also seen in other studies. The basal dichotomy in the Australasian clade is again a result common to all studies. It represents a split between a clade (IIa) consisting of species from New Zealand and New Caledonia, traditionally included in section *Macrocladium* on the one hand, and a clade (IIb) consisting of numerous Australian/Asian species in many other sections on the other. Clements (2006) included a wider sample of New Caledonian species, showing that the sections *Macrocladium*, *Kinetochilus*, *Dendrobates*, *Inobulbium*, *Finetianthe* and *Tetradon* are closely related, but the topology of the subtree is not well supported. The very limited sequence divergence at the higher nodes in this New Caledonian group hardly validates the recognition of so many sections. In Clements's analysis, the New Guinean *D. herpethophyllum* Schltr. (section *Herpethophyllum*) is nested deeply within this clade. In Yukawa's (2001) phylogram, on the other hand, an unidentified species of sect. *Herpethophyllum* resides in a clade with sections *Grastidium*, *Pleianthe* and *Biloba* (syn. sect. *Monanthos*), which agrees much better with morphology and biogeography. As is evident from Clements (2006) and Yukawa (2001), most of the subclades within clade IIb correspond well with morphologically recognised sections, such as *Cadetia*, *Diplocaulobium*, *Brevisaccata* (syn. sect. *Trachyrhizum*), *Crinifera* (genus *Flickingeria*), and *Latouria*. The last, however, is not strongly supported, even when the anomalous position of *D. spectabile* (Blume) Miq. in Clements (2006) is disregarded. In the present study support for clade IIb is much stronger than it is in Clements (2006).

Sections *Spatulata*, *Phalaenanthe* and *Eleutheroglossum* together form a well supported clade that is consistent with morphology. It appears that at least sect. *Phalaenanthe* is nested within sect. *Spatulata* and may not warrant continued recognition.

Another strongly supported, morphologically and biogeographically plausible clade consists of sections *Grastidium* (including *Eriopexis* and *Dichopus*), *Biloba*, *Herpethophyllum* and *Pleianthe*. Not enough species have been sampled to assess the robustness of the sections within this *Grastidium* clade, but the four mentioned here are easily distinguished morphologically.

Two species of section *Fugacia* (syn. sect. *Euphlebiium*) were sampled by Clements (2006). Although this section is well-characterised by vegetative and floral morphology, the two species appear in two separate clades within clade IIb, but without strong support one way or the other.

Sections *Dendrocoryne*, *Monophyllaea* (syn. *Australorchis*) and *Rhizobium* were analysed in detail by Burke et al. (2008) and Adams et al. (2006). Their work suggests that, although morphologically distinct, sections *Rhizobium* and *Monophyllaea* are nested within a broadly defined sect. *Dendrocoryne*. Sect. *Rhizobium* seems to represent a recently evolved clade with xeromorphic adaptations (Yukawa et al. 2000).

Finally, still within clade IIb, Yukawa (2001) finds *D. bulbophylloides* Schltr. of sect. *Microphytanthe* to be sister to *Flickingeria*, but the clade combining these two has low bootstrap support. In Clements's (2006) phylogram *D. bulbophylloides* is sister to *D. toressae* (F.M.Bailey) Dockrill (sect. *Lichenastrum*), with the pair in turn sister to *Flickingeria*, but again with low support.

In summary, in the Australasian clade the sectional classification based on morphology is largely supported by the molecular phylogenies. The relationships between the clades are largely unresolved, however. The position of *Cadetia*, for example, is still unclear.

Turning to the Asian clade (I), the picture is much more confusing. There are several well supported clades, but also quite a few species that do not nest inside any of those clades, e.g., the closely related *D. lindleyi* Steud. and *D. jenkinsii* Wall. ex Lindl., *D. senile* Parish ex Rchb.f., *D. trigonopus* Rchb.f., and *D. capillipes* Rchb.f., which must all be considered unplaced at present. A broad sampling of the florally very similar sections *Dendrobium* and *Densiflora* (syn. sect. *Callista*) by Wongsawad et al. (2005) confirmed that sect. *Densiflora* is polyphyletic, as found by earlier studies (e.g., Yukawa 2001), with *D. chrysotoxum* deeply nested in a well-supported clade that contains species of sect. *Dendrobium* and sect. *Breviflores*. Two other clades of sect. *Densiflora* are each strongly supported, one consisting of the species pair *D. lindleyi* and *D. jenkinsii*, the other consisting of the relatives of *D. densiflorum* Wall. ex Lindl. (clade D in Fig. 2). However, the position of these clades within the Asian clade is still undetermined. It is hard to explain how the continental Asian *D. densiflorum* alliance could be sister to *D. sect. Amblyanthus*, a morphologically quite different section with a predominantly East Malesian distribution, and not to one of the much more similar clades from continental Asia. Yet, this is suggested by the analyses by Yukawa (2001), Wongsawad et al. (2005) and the ITS-based analysis of Sathapattayanon (2008), although not by her matK-based analysis. It should be noted that branch lengths inferred from ITS sequences in the *D. densiflorum* clade and in the *Amblyanthus* clade are much shorter (by about a factor 0.5) than in the neighbouring clades, for instance the second *Pedilonum* clade (clade P2 in Fig. 2) mentioned below. This could be a factor in explaining the rather counterintuitive position of clade D. Section *Dendrobium* is largely supported by Wongsawad et al.'s study, except for a few species (Wongsawad et al.'s clade 7, here represented by *D. capillipes* in Fig. 2) that form a small, rather inexplicably unplaced group outside the main *Dendrobium* clade. Section *Breviflores*, still according to Wongsawad et al., is polyphyletic, and should probably be included in sect. *Dendrobium*.

Section *Formosae* has recently been analysed in detail by Sathapattayanon (2008), who found that the section as traditionally circumscribed falls apart into two distinct sections next to two morphologically aberrant species that have to remain unplaced for the time being (*D. trigonopus* and *D. jerdonianum* Wight). The core of sect. *Formosae* forms a well-defined monophyletic group of some 40 species. The sections *Distichophyllae* and *Conostalix* are, according to ITS data, sister to the as-yet-unnamed clade split off from sect. *Formosae*, but not according to matK data.

Section *Stachyobium* is a strongly supported clade with high sequence divergence. Its position within the Asian clade varies more than any other subclade in the various studies here cited, and this morphologically distinctive section must be considered unplaced.

Perhaps the greatest problem in the Asian clade is presented by the species of the sections *Pedilonum*, *Calcarifera*, *Oxyglossum*, *Calypstrochilus*, *Platycaulon* and *Dolichophyllum*. It was generally believed that they formed a single, monophyletic alliance within *Dendrobium*. The work of Clements (2003, 2006) suggests, however, that this alliance consists, at the highest level, of two strongly supported clades that are not sister clades. To some extent, these two clades are supported by geography, with one clade, P1 in Fig. 2, being predominantly West Malesian (this clade includes the type species for sect. *Pedilonum*, *D. secundum* (Blume) Lindl.), and the other, P2 in Fig. 2, being predominantly East Malesian. However, section *Platycaulon*, which falls in the West Malesian clade, is well represented in East Malesia. There are few, if any, morphological characters that can serve to distinguish P1 and P2. Species of the sections *Pedilonum* and *Calcarifera*, as traditionally understood, are found both in clade P1 and in P2.

The sister clade to P2 is a strongly supported alliance consisting of the sections *Crumenata*, *Aporum*, *Strongyle* and *Bolbodium*. This clade is probably best considered as a single section (to be called *Aporum*), because species with virtually identical, ephemeral flowers occur in each of the four sections. There is some support, however, for a subdivision into two subgroups, one having stems with a few swollen internodes, the other having stems without any swollen internodes. Section *Bolbodium* is nested within sect. *Crumenata*, and appears to represent a case of vegetative reduction or neoteny. The *Aporum* clade and clade P2 together form a strongly supported clade in all studies.

In summary, the Asian clade contains several well-supported subclades, but these are much less congruent with morphology than in the Australasian clade, and the relations between the subclades are, in many cases, still unclear.

Discussion

Do these results, and the studies cited here, support the splitting up of *Dendrobium* into smaller genera? To some extent they do, in that the three basal clades in the Dendrobiinae would at first sight be good candidates for recognition at genus level. Not only are they well supported, there is also a distinct geographical signal present. Unfortunately, there appear to be no consistent morphological characters to distinguish between the Asian clade and the Australasian clade. Both groups, if recognised as separate genera, would be highly heterogenous and an identification key for these two entities would be too complex to be useful. Therefore, if splitting is considered desirable, then this has to occur at lower levels. But, as I have pointed out repeatedly above, the delimitation of several clades is still problematic. There are unplaced species, there are fragmented morphology-based sections, and there are strongly supported clades that,

if recognised as genera, would be very hard to distinguish from other genera. There is, beyond the level of the three basal clades, no obvious way to split up *Dendrobium* into monophyletic genera.

Apart from these practical difficulties, there are several arguments that can be invoked in favour of, or against splitting. The main arguments in favour of splitting, mostly paraphrased from Clements (2003, 2006), are:

1. A very large genus of more than 1500 species is impractical; it makes species-identification more difficult and membership of such a large genus conveys little information about the characters of any particular species.
2. Many clades are very distinctive, and some have already been recognised at genus level for a long time, such as *Cadetia* and *Flickingeria*.
3. It is inconsistent to have numerous small genera in one large subtribe, such as the Aeridinae, and only one big genus in another, even larger one.
4. Splitting is unavoidable, because the group under consideration is polyphyletic.

These are some possible counter arguments:

1. A large genus may be impractical, but so is a large number of genera that are difficult to distinguish.
2. Many clades are not distinctive at all.
3. There are no rules for the size of genera. The size of a genus depends on a specific, historical pattern of speciation and extinction, therefore a wide range of sizes among different genera is to be expected. Moreover, the number of recognised genera in the Aeridinae is probably far too large.
4. After the removal of *Pseuderia* and *Oxystophyllum*, the polyphyly argument no longer applies to *Dendrobium*.

The main arguments against splitting are as follows:

1. There is no obvious 'best' way to split *Dendrobium* into smaller genera.
2. Splitting is at any rate premature because the presently available phylogenies show too little resolution, and the sampling has been inadequate for most sections.
3. While many of the segregate genera are easily recognised (*Cadetia*, *Diplocaulobium*), others would be hard to distinguish, even by specialists.
4. Splitting will result in a huge number of name changes, rendering older publications obsolete and herbarium management more difficult. Reassigning *Cadetia* and other segregates back to *Dendrobium* will do this to a far lesser extent.
5. The horticulturally extremely important *D. bigibbum* and its hybrids will no longer belong to the genus *Dendrobium*.
6. The popular image of taxonomists as people who endlessly tamper with well-established names will be confirmed.

All arguments considered, and recognising that one of the few objective criteria that may guide us in the delimitation of genera is the criterion of monophyly, it seems to me preferable to take a broad view of *Dendrobium*, and to include in it all the former segregate genera (except *Pseuderia* and *Oxystophyllum*). In principle, the genus *Epigeneium* could be kept as a separate genus, as it is sister to all the other species in the Dendrobiinae. However, morphologically *Epigeneium* is not particularly distinctive when compared with such species as *Dendrobium carriei* Rupp & C.T.White.

Inclusion of *Epigeneium* would not add any new character states, or even any obvious combinations of character states to *Dendrobium*. Therefore, apart from its status as sister genus, there are hardly any solid arguments to maintain this relatively small genus of some 40 species next to the huge conglomerate of *Dendrobium*. There is also no particularly large sequence divergence between *Epigeneium* and the rest of *Dendrobium*.

The case of *Dendrobium* is not unique: similar problems are posed by other very large orchid genera including *Bulbophyllum*, *Epidendrum*, *Eria*, *Habenaria*, and *Pleurothallis*, among others. In the case of *Eria* and *Pleurothallis*, the arguments in favour of splitting have prevailed (Pridgeon et al. 2005), and in my opinion rightly so, since the formerly broadly defined genera were clearly highly polyphyletic. Generic delimitation is still debatable in some cases. Splitting of *Epidendrum* (Pridgeon et al. 2005) and *Bulbophyllum* (Vermeulen, pers. comm.) has so far not been favoured by modern experts in these genera. At least in the case of *Bulbophyllum*, the arguments are very much like those listed above for *Dendrobium*, except that *Bulbophyllum* has far less significance in horticulture.

Character evolution and the origin of Dendrobium

Roughly speaking, there are two main habit types in *Dendrobium*: plants with pseudobulbs and plants with cane-like stems. This is an oversimplification, as there are many intermediate cases, but it does raise the question what the earliest dendrobiums looked like. I believe the molecular phylogenies enable us to answer this question. We now know that the *Epigeneium* clade is sister to all the other *Dendrobium* species, and we also know that *Bulbophyllum* is sister to *Dendrobium s.l.* All *Bulbophyllum* species have heteroblastic pseudobulbs with one or two, non-sheathing apical leaves. The same is true for *Epigeneium*. Moreover, *Epigeneium* has distinct, creeping rhizomes, a character-state also found in numerous *Bulbophyllum* species. These facts suggest that the earliest dendrobiums were plants with heteroblastic pseudobulbs with one or two terminal, non-sheathing leaves and creeping rhizomes. Species, indeed whole sections, with such a habit are still found in the Australasian clade, for example in sections *Diplocaulobium*, *Rhizobium*, *Microphytanthe*, and others. However, they are not basal in this clade, and are absent from the Asian clade. This suggests that the most recent common ancestor to the Asian and Australasian clade was a plant with a cane-like habit, and that cases like *Diplocaulobium* represent reversals to the earliest ancestral type.

How early were those earliest ancestors? There are various theories about the origin of *Dendrobium*. The clear split between an Asian and an Australasian clade (or what Wood (2006) refers to as the Northern and Southern clade) has led some authors (Brieger 1981, Wood 2006) to propose a very early origin for *Dendrobium*, as they invoke the splitting up of Gondwanaland (around 60–70 million years ago) to explain the existence of the two clades. However, if that were the case, then one would expect far greater sequence as well as morphological divergence between the two clades than is actually observed. A more recent origin in continental Asia, or possibly Africa, with subsequent dispersal to Australia, New Caledonia and New Zealand, as advocated

by Lavarack et al. (2000), seems more plausible. Dispersal in the opposite direction would explain why certain members of the Australasian clade are in fact better represented in the western (Asian) part of the range of *Dendrobium*, in particular sect. *Crinifera* (the former genus *Flickingeria*). The radiation of clade P2 in New Guinea may be the result of a relatively recent secondary west-to-east dispersal. The complex geology of Wallacea, with land rapidly appearing and disappearing within a few million years around 10 million years ago (Hall 2009), may explain these secondary dispersals. As for the primary dispersal from Asia to Australia, New Caledonia, and New Zealand, this must have occurred more than 23 million years ago, assuming that a recently discovered, c. 23 million year old fossil from New Zealand described as *D. winikaphyllum* Conran, Bannister & Lee (Conran et al. 2009), is indeed a *Dendrobium* species. Gustaffson et al. (2010), using this fossil to provide a calibration point, dated *Dendrobium* to about 32 mya, with a 95% confidence interval of 25 to 40 my.

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